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Genetic control of pulp and timber properties in maritime pine (*Pinus pinaster* Ait.)

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Abstract – Wood is one of our most important natural resources and has been exploited for many hundreds of years as fuel, building material and a source of paper. Its composition is variable among and within species. The ability to monitor the intra-specific variability is a prerequisite to improve wood and end-products properties. This paper describes a study of the genetic control of a large set of wood properties, including growth, timber quality traits, wood chemical composition, kraft pulp production parameters and pulp properties, in a 12×12 half diallel of maritime pine (*Pinus pinaster* Ait.). While relatively high ($h_{ns}^2 > 0.3$) narrow-sense heritabilities were observed for density heterogeneity, lignin content, alpha-cellulose content and coarseness, no significant genetic effect was detected for hemi cellulose, water extractives, kraft pulp production parameters and pylodin. Slightly lower heritabilities ($0.15 < h_{ns}^2 < 0.3$) were also obtained for wood density and fibre properties (length, width, curl, zero span). As a consequence and considering the phenotypic coefficient of variation obtained for these traits, improvement by selection of trees with outstanding wood quality is feasible. Nevertheless, it seems obvious that wood quality breeding can not be done without taking into account growth, and the only way to manage this constraint (negative correlation between growth and density) will be the constitution of elite "wood quality" populations in a already growth improved genetic population.

wood quality / heritability / genetic correlation / tree breeding / *Pinus pinaster* Ait.

Résumé – Déterminisme génétique des propriétés du bois impliquées dans la production papetière et la qualité du bois d'œuvre chez le Pin maritime (*Pinus pinaster* Ait.). Le bois, une des ressources naturelles les plus importantes, est exploité depuis des centaines d'années comme combustible, matériau de construction et source de papier. Sa composition est très variable, non seulement entre espèces mais aussi au niveau intra spécifique. La compréhension de cette variabilité intra spécifique est un pré-requis de l'amélioration des propriétés des produits à base de bois. L'objectif de l'étude présentée ici est la compréhension du déterminisme génétique de plusieurs caractères impliqués dans la composition chimique et les propriétés du bois (caractéristiques physiques, paramètres de production industrielle et propriétés de la pâte) grâce à l'étude d'un demi diallèle 12×12. Bien que des héritabilités au sens strict relativement élevées ($h_{ns}^2 > 0,3$) aient été obtenues pour l'hétérogénéité de la densité, les contenus en lignine et en alpha-cellulose et la masse linéique, aucun effet génétique significatif n'a été mis en évidence pour le contenu en hémi-cellulose, les extractibles, les paramètres de production de pâtes kraft, et la densité estimée grâce au pilodyn. Des héritabilités plus faibles ($0,15 < h_{ns}^2 < 0,3$) ont quant à elles été obtenues pour la densité du bois et les propriétés des fibres (longueur, largeur, courbure, rigidité). En conséquence, considérant les coefficients de variation phénotypiques obtenus pour ces caractères, des gains génétiques significatifs peuvent être attendus. Néanmoins, l'amélioration des propriétés du bois ne pourra pas se faire sans prendre en compte la croissance. Le seul moyen de gérer cette contrainte (induite par des corrélations négatives entre croissance et densité) sera la constitution de populations élites pour la qualité du bois au sein de bases génétiques déjà améliorées pour la croissance.

qualité du bois / héritabilité / corrélation génétique / amélioration / *Pinus pinaster* Ait.

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1. INTRODUCTION

Wood can be regarded as a natural composite material consisting of flexible tubes of cellulose bonded together and held rigid by lignin. However, this simple definition hides the fact that wood is also highly complex and variable, not only in its chemical composition but also at the anatomical level (e.g. tracheid morphology). This variability, which occurs not only between species, but also within a species and even within a single tree, is double-edged. On the one hand it allows wood to be utilised for many kinds of products (papers, building materials, chemicals, energy, etc.), but on the other hand it compromises its performance in each application. The understanding of this variability and our ability to use it are of key importance in order to improve the end-use products.

Maritime pine (*Pinus pinaster* Ait.) is an important commercial species in southwest Europe. It is the primary coniferous species in France in terms of planted area (1.4 million ha) and harvest yield (8.3 millions m^3 per year). Its wood is used in both the timber and pulp industries, involving different partners (forest owners, timber and pulp industrials) for whom different traits may be of interest. Today, the maritime pine breeding programme has achieved its third generation of selection. Genetic gain of improved varieties is about 30% for both volume and straightness. The introduction of wood quality selection criteria is now considered as an important objective of the breeding programme. Such selection is however hampered by the lack of information for wood quality traits, not only at the genetic but also at the industrial levels.

Wood quality can only be defined in terms of particular end use, and may involve several traits (e.g. density, wood heterogeneity, wood chemical composition and fibre properties). Mean density is acknowledged to be the best single predictor of wood mechanical properties [1, 36, 41, 43, 48, 67]. Fairly strong positive correlations between modulus of elasticity (MOE), a basic mechanical property of softwoods, and density have often been reported (for review see [54]). But, in spite of its key importance, mean density is not the only trait involved in wood mechanical properties. Larson [33] stated that the greatest wood quality problems facing all wood-using industries is lack of uniformity. With respect to density, according to Megraw [38], "the greatest variability in specific gravity occurs within each annual ring". Thus one of the targets of breeding for wood mechanical properties could be a decrease in density heterogeneity within individual rings. This modification might also affect pulp production if within-ring heterogeneity in density was associated with heterogeneity of chemical and fibre properties. It is assumed that wood density is positively linked to pulp yield (increasing density also increase the tonnage of dry fibre produced per unit area), and some pulp quality traits [9, 22, 25, 28]. Unfortunately, wood density alone is a poor indicator of other kraft pulp quality traits [28, 29]. In order to estimate the "pulp potential" of a tree, it is important to take into account its fibre characteristics. Recent studies have shown that several fibre properties can have a pronounced influence on pulp yield and pulp quality [16, 25, 27, 68]. The chemical composition (e.g. lignin, polysaccharides, extractives) must also be considered, these traits have direct consequences for production costs and final product quality.

Breeding trees to produce wood for a given wood processing industry is a complex problem. It is essential (1) to define which are the key properties influencing the quality of the product, (2) to estimate the possibilities of genetic improvement of these key properties and (3) to estimate the correlated response to selection for key properties of other targeted traits such as growth. In order to provide the background for initiating a breeding programme for wood quality in maritime pine, genetic parameters are being estimated for a large set of wood properties in a wide range of experimental designs (diallel, factorial and clonal tests). This paper describes a study of the genetic determinism of a large set of wood properties in a half diallel. Genetic parameters including heritabilities and genetic correlations are presented and a breeding strategy for the utilisation of maritime pine wood for timber and pulping purposes is discussed.

2. MATERIALS AND METHODS

2.1. Experimental trial

A 12×12 half-diallel was used to estimate the phenotypic variability and the genetic parameters (variance components, heritabilities and genetic correlations) of the studied traits. Parental trees were mated in 1980, seeds from the controlled crosses were sown in a nursery in spring 1982 and seedlings were planted in autumn 1982. The 12 parents were "plus trees", phenotypically selected for stem growth and straightness in the local provenance of the Landes de Gascogne. The half-diallel was located in Cestas (Gironde, France, $0°$ 44' W, $44°$ 44' N) on a semi-humid podzolic soil. Spacing was 4 m between rows and 1.1 m between individual trees, i.e. 2272 trees/ha. The experimental design consisted of 74 incomplete randomised blocks. Each block comprised 16 plots of 4 trees. For the present study, 591 trees belonging to 73 families (without selfed crosses) were cut in March 1997 (when trees were 14 years old). The fact that 73 families were involved in the half-diallel (without selfed crosses) analysis instead of 66 was due to the low number of individuals for some families. Assuming that maternal effects were low at 15 years of age [18], some families from the opposite half-diallel were introduced in order to improve the power of our analysis. Each family consisted of eight individuals on average.

2.2. Data measurement

Five types of traits namely (1) growth, (2) timber quality traits, (3) wood chemical composition, (4) kraft pulp production parameters and (5) fibre properties were measured. For each trait, the number of individuals measured, the mean and the phenotypic coefficient of variation are given in *table I*.

Before felling, straightness (**STR**) was estimated as the deviation of the tree from verticality at 1.3 m. This data is given in cm, and increases with the divergence of the tree from verticality. At the same

Table I. Definition, number of observations (n), mean value (mean) and phenotypic coefficient of variation (CV_p) of the studied traits.

	Traits	Definition	Unit	n	Mean	CV_p(%)
Growth	TH	Total height at 14 year-old	cm	575	982.81	12.07
	STR	straightness	cm	589	17.05	60.41
Timber quality	d	mean density of all the rings	kg m^{-3}	566	413.69	7.41
	pyl	pilodyn penetration	mm	428	19.32	8.77
	het	mean standard deviation of all rings	kg m^{-3}	567	106.68	11.87
	lignin	lignin content measured by FTIR	%	566	28.99	4.06
	wext	water extractives content	%	566	6.56	33.43
Wood chemical composition	aext	acetone extractives content	%	566	0.59	90.15
	alfacel	alpha cellulose content	%	554	46.37	2.87
	hemicel	hemi cellulose content	%	554	24.21	1.78
Kraft pulp production parameters	resalk	residual effective alkali	g L^{-1}	580	3.88	38.06
	PulpY	kraft pulping yield adjusted to the kappa number	%	581	43.78	4.00
	kappa	kappa index	%	581	31.54	10.40
	afl	arithmetic fibre length	mm	575	0.65	8.60
	wfl	weighted fibre length	mm	575	1.86	7.49
	fw	fibre width	μm	575	27.83	2.14
Fibre properties	coars	coarseness	μg mm^{-1}	575	0.14	7.93
	curl	curl index	%	575	7.46	7.80
	zspan	zero span tensile value	N cm^{-1}	541	8351.90	16.28

time, pilodyn pin depth of penetration (**pyl**), an indirect estimation of wood density [23], was measured at breast height under bark. In order to avoid compression wood, the pilodyn was applied on the opposite radii perpendicular to the prevailing wind direction. After felling, total height (**TH**) of each tree was recorded and three logs were cut above 1.3 m from the ground in order to minimise root system influences on characterization of wood properties.

The first log (7 cm in length) was used for detailed X-ray densitometry measurement using the method described by Polge [50]. The wood sample was chosen in order to avoid compression wood. Based on the X-ray microdensitometric profiles, mean (**d**) and heterogeneity of density (mean of ring standard deviation of density) (**het**) were calculated.

Wood chemical properties were estimated on the second log (10 cm in length). Two successive extractions were carried out on wood powder, first with water (**wext**) and then with acetone (**aext**) in order to quantify the proportion of extractable components (tannins, resins, fatty acids...). Lignin (**lignin**), hemicellulose (**hemicel**) and alpha cellulose (**alphacel**) contents of oven-dry extractive-free wood were predicted by using a calibration model relating FTIR (Fourier Transform Infrared spectroscopy) data with values obtained by traditional chemistry methods. The applied calibration and prediction procedure are reported by Rodrigues et al. [51].

The third contiguous log (40 cm in length) was turned into chips, stabilised in a controlled climate cell to a constant dry matter content of 89%, and extracted according to the procedure described above. Then, samples were kraft pulped to kappa 30 in 150 mL digesters using the following cooking programme: 90 minutes from 20 °C to 170 °C, 90 minutes at 170 °C; white liquor 24% active alkali, 30% sulfidity, liquor/wood ratio of 4. The residual concentration of NaOH in the black liquor after pulping, also called residual effective alkali (**resalk**), kappa index (**kappa**), used to assess the degree of delignification of the pulp kraft, and pulping yield adjusted (by covariance analysis) to the kappa index (**PulpY**) (%) were measured.

After pulping, fibre characteristics were determined using PQM 1 000 apparatus. Measurements were made on samples of 2 g of pulp (equivalent oven-dry weight). Fibre properties were arithmetic mean fibre length (**afl**), weighted mean fibre length (**wfl**) (which reduces the effect of small fragments of fibres), fibre width (**fw**), coarseness (**coars**) (a measure of mass per unit length of fibre) and curl index (**curl**) (measured as [real length/projected length-1] × 100 which is an assessment of the straightness of the fibres). Finally average tensile strength of individual fibres (**zspan**) was derived from the measurement of the wet zero-span tensile value using TAPPI method: T273 pm-95 [59].

2.3. Parameters estimation procedure: half-diallel analysis

Genetic parameters were estimated using the DIOGENE software [2, 3].

In the first step, analysis of variance for block, family and block × family interaction effects derived from a "Henderson III" model [56] was carried out. Linear model assumptions were checked for each trait. When necessary, data were adjusted for the block effect, prior to the decomposition of the family effect (half-diallel analysis). In the second step, analysis of the half-diallel (selfed combinations were not considered) was carried out using the following random model:

$$Y_{ijk} = \mu + a_i + a_j + s_{ij} + \varepsilon_{ijk}$$

where Y_{ijk} is the value of the trait for the individual k corresponding to the cross between the male i and the female j, a_i (a_j) is the general combining ability (GCA) of the i-th (j-th) parent, s_{ij} is the specific combining ability (SCA) of the cross between the i-th and the j-th parent and ε_{ijk} is the residual term. The additive and dominance variances are: $\sigma_A^2 = 4\sigma_a^2$ and $\sigma_D^2 = 4\sigma_s^2$ and and the phenotypic variance is: $\sigma_P^2 = \sigma^2(Y_{ijk}) = \sigma_a^2 + \sigma_s^2 + \sigma_\varepsilon^2$.

2.4. Heritabilities

Epistatic variance components were assumed to be small enough to be ignored and narrow (ns) and broad sense (bs) heritabilities were calculated as $h^2_{ns} = \sigma^2_A / \sigma^2_P$ and $h^2_{bs} = (\sigma^2_A / \sigma^2_D) / \sigma^2_P$, respectively.

2.5. Correlations

Estimates of covariance between pairs of traits were derived from a multi-trait analysis of covariance. Subsequently the corresponding correlation estimates were calculated as follows:

$$r_{xy} = \sigma_{xy} / (\sigma_x \cdot \sigma_y)$$

where x and y indicate two different traits.

Accuracies of the estimates of genetic parameters were obtained by bootstrap analysis (1 000 samples for each parameter). The normality of the distributions obtained were checked and 95% confidence intervals (CI) were calculated as CI = μ ± 1.96 σ (where μ is the mean and σ the standard deviation of the parameter values obtained by bootstrapping).

2.6. Breeding parameters

Expected genetic gains (GG) were calculated for each trait (x) according to the following formula:

$$GG_x = i \cdot h^2_{ns} \cdot \sigma_{Px}$$

where i is the selection intensity; h^2_{ns} is the narrow sense heritability and σ_p the phenotypic standard deviation of trait x.

Selection for one trait (x) will result in a correlated response of other traits, and the correlated response of a trait y can be estimated by using the equation of indirect response [17]:

$$Cr_{y/x} = i \cdot h_x \cdot h_y \cdot rg_{xy} \cdot \sigma_{Py}$$

where $Cr_{y/x}$ is the correlated response of trait y due to selection for trait x, h_x and h_y are the square roots of appropriate narrow sense heritabilities for traits x and y respectively; rg_{xy} is the additive genetic correlation between traits x and y and σ_{py} is the phenotypic standard deviation of trait y.

Finally, because of the high number of traits contributing to wood quality and the general requirement of forest tree users for multi-uses varieties instead of single-use ones, multi trait selection was examined according to the method presented by Lin [35].

3. RESULTS

3.1. Phenotypic variation and decomposition of the genetic variance

For each trait, descriptive statistics are given in *table I*. Total height (**TH**) and straightness (**STR**), the two selection criteria of the current maritime pine breeding programme showed moderate to high coefficients of phenotypic variation: 12.07 and 60.41%, respectively. These results are consistent with those of previous studies in maritime pine [12, 31]. With the exception of extractives content (**aext**, **wext**), which exhibited high levels of phenotypic variation, the phenotypic coefficients of variation for wood quality traits were low (less than 10%). This is consistent with most of the results reports in the literature [11, 30, 44, 45].

The model, including block and family, allowed us to detect significant genetic controls for thirteen of the nineteen studied traits (*table II*). On average, the genetic effect

Table II. Analysis of block, family and family × block interaction.

Source	Block			Family			Family ×Bloc		
df	73			72			201		
Traits	F	*P*-value (%)	r^2 (%)*	F	*P*-value (%)	r^2 (%)*	F	*P*-value (%)	r^2 (%)*
TH	**3.96**	**0.00 s**	**37.99**	**2.48**	**0.00 s**	**24.44**	**1.73**	**0.01 s**	**27.16**
STR	1.06	36.71 ns	12.16	**3.03**	**0.00 s**	**35.70**	1.05	37.47 ns	32.50
d	1.06	37.44 ns	13.93	**1.88**	**0.02 s**	**25.45**	1.02	46.13 ns	37.36
het	1.29	8.02 ns	15.02	**2.76**	**0.00 s**	**33.07**	1.10	24.95 ns	32.98
resalk	1.88	0.02 s	23.83	1.29	7.97 ns	16.82	0.97	58.57 ns	35.96
PulpY	1.46	1.71 s	21.32	0.88	74.48 ns	13.08	1.07	32.44 ns	41.17
kappa	0.84	81.14 ns	13.27	0.98	53.05 ns	15.94	1.09	26.85 ns	44.81
lignin	**1.38**	**3.74 s**	**16.31**	**2.43**	**0.00 s**	**29.46**	1.02	45.46 ns	33.45
wext	1.30	7.32 ns	19.97	1.05	39.43 ns	16.50	1.37	1.40 s	43.47
aext	0.98	53.02 ns	13.03	**1.47**	**1.53 s**	**20.18**	0.82	92.61 ns	37.68
alfacel	1.01	46.481 ns	13.92	**1.66**	**0.23 s**	**23.52**	1.05	37.95 ns	39.00
hemicel	0.924	68.848 ns	14.58	1.14	22.54 ns	18.57	1.28	4.63 s	44.70
wfl	1.20	15.69 ns	15.89	**1.76**	**0.08 s**	**23.92**	1.05	37.56 ns	37.52
afl	1.15	21.81 ns	15.61	**1.64**	**0.29 s**	**22.85**	1.05	35.99 ns	38.45
fw	1.18	18.50 ns	15.22	**1.81**	**0.04 s**	**24.09**	0.97	60.10 ns	36.69
coars	1.07	35.53 ns	12.86	**2.46**	**0.00 s**	**30.54**	0.96	60.85 ns	34.18
curl	0.84	80.82 ns	12.97	**1.47**	**1.55 s**	**23.39**	**1.39**	**1.00 s**	**43.71**
zspan	**1.36**	**4.51 s**	**18.90**	1.48	1.50 s	21.14	1.19	11.39 ns	39.17
pilodyn	1.08	33.11 ns	13.04	1.14	19.47 ns	21.11	1.26	6.02 ns	46.06

* r^2 (%) is the proportion of the variance accounted by the considered term in the model.

Table III. Decomposition of the genetic variance: significance of additive and dominance effects.

Source	GCA			SCA		
df	11			51		
Traits	F	p-value (%)	r^2 (%)*	F	p-value (%)	r^2 (%)*
TH_adj	8.561	0.00 s	24.78	1.869	0.05 s	13.42
STR	5.561	0.00 s	13.80	1.326	7.07 ns	11.51
d	8.341	0.00 s	15.88	1.009	46.03 ns	8.83
het	13.831	0.00 s	26.15	1.16	21.68 ns	8.77
lignin_adj	13.404	0.00 s	23.12	1.074	34.54 ns	10.13
alfacel	11.44	0.00 s	24.76	0.83	79.314 ns	10.04
aext	1.932	5.65 ns	5.05	1.102	29.79 ns	0.24
wfl	4.768	0.01 s	11.54	1.25	12.22 ns	11.22
afl	1.314	0.02 s	10.77	1.284	9.67 ns	11.58
fw	5.532	0.00 s	10.85	0.978	52.09 ns	9.09
coars	10.908	0.00 s	19.91	1.017	44.46 ns	8.46
curl	8.662	0.00 s	13.83	0.809	82.52 ns	7.40
zspan_adj	3.495	0.11 s	10.18	1.524	1.51 s	13.51

* r^2 (%) is the proportion of the varaiance accounted by the considered term in the model.

Table IV. Estimated narrow sense (h^2_{ns}) and broad sense (h^2_{bs}) heritabilities (with their confidence interval).

	h^2_{ns} (confidence interval)	h^2_{bs} (confidence interval)
TH_adj	0.456 (0.321–0.592)	0.727 (0.490–0.963)
STR	0.231 (0.108–0.354)	non significant SCA effect
d	0.295 (0.167–0.422)	"
het	0.509 (0.371–0.646)	"
lignin_adj	0.471 (0.334–0.608)	"
alfacel	0.343 (0.227–0.458)	"
wfl	0.19 (0.08–0.299)	"
afl	0.172 (0.059–0.285)	"
fw	0.184 (0.071–0.298)	"
coars	0.374 (0.240–0.509)	"
curl	0.249 (0.124–0.374)	"
zspan_adj	0.16 (0.042–0.278)	0.373 (0.105–0.642)

Table V. Expected genetic gain for each trait considered independently for a selection intensity of 5%, genetic gain given in trait units (GG) and in percent (GG%).

	GG trait unit	GG%
TH_adj	111.63	11.36
STR	4.91	28.79
d	18.65	4.51
het	13.30	12.46
lignin_adj	1.14	3.95
alfacel	0.94	2.03
wfl	0.05	2.94
afl	0.02	3.05
fw	0.23	0.81
coars	0.01	6.12
curl	0.30	4.01
zspan_adj	448.75	5.37

accounted for 25% of the phenotypic variance. For three of the traits (**TH**, **lignin** and **zspan**) showing a significant genetic effect, a significant block effect was also detected; the raw data for these traits were adjusted prior to the decomposition of their genetic variance, (**TH_adj**, **lignin_adj** and **zspan_adj**).

Results of the genetic variance decomposition are shown in *table III*. Surprisingly, although a significant family effect ($P = 1.53\%$) was detected for acetone extractives (**aext**), a non-significant GCA variance ($P = 5.68\%$) was observed for this trait. This can be explained by the structure of the two models employed for statistical analysis: these used different denominators and degrees of freedom to determine the significance of effects. For the other traits, with the exception of total height (**TH_adj**) and zspan (**zspan_adj**) for which significant dominance effects were observed, only additive genetic effects were detected. The GCA variance observed accounting for 10 to 26% of the phenotypic variation.

3.2. Genetic control

Narrow and broad-sense heritabilities and their confidence intervals are shown in *table IV*. Total height (**TH_adj**), which is used traditionally as a predictor of growth, had narrow and broad sense heritabilities of 0.456 and 0.727, respectively. These results underlined, as already demonstrated in the current maritime pine breeding programme, the possibility of obtaining high genetic gains by exploiting dominance as well as additive components of genetic variation.

Apart from lignin content which exhibited a relatively high narrow sense heritability (0.471), the wood quality traits showed generally low to moderate values (ranging from 0.16

for zero span to 0.374 for coarseness). Among the wood quality traits, zero span was the only trait for which dominance effects could be used to improve selection efficiency.

3.3. Expected genetic gains

Expected genetic gains were calculated for a selection intensity of 5% (*table V*). Although high genetic gains (> 10%) can be obtained for the traditional targeted traits of the maritime pine breeding programme (**TH_adj** and **STR**), expected genetic gains are generally lower (less than 5%) for wood quality traits. Only wood heterogeneity (**het**) gives expected gains of more than 10%.

3.4. Genetic correlations and correlated responses to selection

Amongst those traits for which genetic effects were not significant (*table II*), non significant or low (most of the time

Table VI. Phenotypic correlations (r_p) between traits not under genetic control, growth (TH_adj) and density (d).

Trait1	Trait2	r_p
TH_adj	**pilodyn**	**–0.18**
TH_adj	resalk	–0.016 ns
TH_adj	PulpY	–0.11
TH_adj	**kappa**	**–0.093**
TH_adj	wext	–0.035 ns
TH_adj	aext	0.067 ns
TH_adj	**hemicel**	**–0.19**
d	**pilodyn**	**–0.13**
d	**resalk**	**0.177**
d	PulpY	0.066 ns
d	kappa	0.041 ns
d	**wext**	**–0.108**
d	aext	0.001 ns
d	hemicel	0.083 ns

* ns: not significant at 5% level.

Table VIII. Phenotypic (r_p) and additive genetic (r_a) correlations between growth (TH_adj) and wood quality traits, and breeding consequences.

Trait	r_p [a]	r_a [b]	CR [c]	CR% i [d]	CR 1% HT [e]
TH_adj	1	1	111.63	11.36	1.00
STR	0.169	0.343 ns	2.37	13.87	1.22
d	–0.192 ns	**–0.48**	–11.13	–2.69	–0.24
het	0.044 ns	–0.085 ns	–1.07	–1.00	–0.09
lignin_adj	–0.053 ns	**0.395**	0.44	1.53	0.14
alfacel	0.151	**–0.366**	–0.4	–0.86	–0.08
wfl	0.203	0.361 ns	0.03	1.64	0.14
afl	0.278	**0.795**	0.03	3.95	0.35
fw	–0.048 ns	0.064 ns	0.02	0.08	0.01
coars	0.278	**0.429**	0.00	2.90	0.26
curl	–0.299	–0.184 ns	–0.07	–1.00	–0.09
zspan_adj	–0.057 ns	**–0.432**	–327.27	–3.92	–0.34

[a] Phenotypic correlation.
[b] Additive genetic correlation.
[c] Correlated response (in trait units) to selection for height (proportion selected 5%).
[d] Correlated response (in %) to selection for height (proportion selected 5%).
[e] Correlated response (in %) for a height improvement of 1% (proportion selected 5%).
*ns: not significant at 5% level

lower than 0.15) phenotypic correlations were observed with height and density (*table VI*). Even the correlation between density and pilodyn measurements was low.

Because of the predominance of additive effects for the traits under genetic control, only additive genetic correlations are presented. First, given the importance attributed to fibre properties and wood chemical composition in determining pulp and paper properties, the correlations among these traits were calculated. Then, in order to estimate correlated responses to selection, the outcomes of two strategies were simulated: (1) the consequences of selection for height on wood quality traits; (2) the correlated responses of other wood quality and growth traits to selection for wood density.

Fibre morphology traits (fibre length and width) were highly correlated (*table VII*). Moreover, strong genetic correlations were observed between fibre dimensions and coarseness (positive correlation) and between fibre dimensions and curl index (negative correlation). Although fibre morphology (length, width, coarseness) was generally independent of wood chemical composition, curl was highly correlated with

lignin (–0.54) and α-cellulose content (+0.567). Similarly, as found in a study of the maritime pine breeding population (G. Chantre, AFOCEL, France, unpublished) and in *Pseudotsuga menziesii* [10], a strong negative correlation was observed between lignin and α-cellulose contents.

A negative genetic correlation (–0.48) was observed between height and mean density. Thus, selection for growth alone will have negative consequences for solid wood properties, as shown in *table VIII*. For a 1% growth improvement, density will be decreased by 0.24%. This type of selection will also have significant impacts on the chemical composition of wood and on fibre properties (*table VIII*), with an increase in the lignin/α-cellulose ratio, fibre size and coarseness but a decrease in fibre strength.

The correlations obtained between density, growth and wood properties (*table IX*), suggest that selection for wood density alone would severely decrease growth (0.97% growth

Table VII. Additive genetic correlations between fibre properties and wood chemical composition.

	wfl	afl	fw	coars	curl	zspan_adj	lignin_adj	alfacel
wfl	1.000	**0.752**	**0.619**	**0.763**	–0.192 ns	0.387 ns	–0.266 ns	0.229 ns
afl		1.000	**0.556**	**0.939**	**–0.623**	–0.032 ns	0.141 ns	–0.194 ns
fw			1.000	**0.822**	**–0.665**	–0.018 ns	0.261 ns	–0.292 ns
coars				1.000	**–0.766**	0.052 ns	0.122 ns	–0.131 ns
curl					1.000	–0.127 ns	**–0.540**	**0.567**
zspan_adj						1.000	–0.327 ns	0.37 ns
lignin_adj							1.000	**–1.030**
alfacel								1.000

*ns: not significant at 5% level.

Table IX. Phenotypic (r_p) and additive genetic (r_a) correlations between density (d) and wood quality traits, and breeding consequences.

	r_p [a]	r_a [b]	CR [c]	CR% i [d]	CR 1% HT [e]
d	1	1	18.65	4.51	1.00
TH_adj	–0.192	**–0.48**	–43.10	–4.39	–0.97
STR	–0.017 ns	0.101 ns	0.56	3.29	0.73
het	0.098 ns	–0.194 ns	–1.96	–1.84	–0.41
lignin_adj	0.003 ns	**–0.544**	–0.49	–1.70	–0.38
alfacel	–0.032	**0.624**	0.54	1.17	0.26
wfl	–0.229	–0.39 ns	–0.03	–1.43	–0.32
afl	–0.2	**–0.679**	–0.02	–2.71	–0.60
fw	–0.285	**–0.763**	–0.22	–0.79	–0.17
coars	–0.124 ns	**–0.649**	0.00	–3.53	–0.78
curl	0.141	**0.653**	0.21	2.85	0.63
zspan_adj	–0.004 ns	–0.117 ns	–71.29	–0.85	–0.19

[a] Phenotypic correlation.
[b] Additive genetic correlation.
[c] Correlated response (in trait units) to selection for density (proportion selected 5%).
[d] Correlated response (in %) to selection for density (proportion selected 5%).
[e] Correlated response (in %) for a density improvement of 1% (proportion selected 5%).
*ns: not significant at 5% level.

decrease for a 1% density improvement). This type of selection would also result in a decrease of the lignin/α-cellulose ratio, accompanied by a decrease in fibre dimensions and an increase in curl index.

Taking into account the adverse genetic correlations observed among targeted traits (particularly between growth and density), we attempted to define a selection index (*table X*). Utilization of the selection index "A" used currently in the maritime pine breeding programme (simultaneous improvement of both growth and straightness) implies severe reductions in density and α-cellulose content and an increase in lignin content (i.e. a depreciation in the trait, since low lignin content is desirable). Modification of the weight applied to density while keeping growth and straightness coefficients constant (index "B"), generated in the best case a close-to-zero genetic gain for growth, an improvement in straightness (43.71% of the maximum expected gain for this trait) and an increase in density corresponding to 52% of the maximum expected gain for this trait.

A maximum increase in density with no consequences for growth (index "C") reduces straightness and increases density by 6.1%, which correspond to 80% of the maximum possible genetic gain for this trait. Finally index "D", combining constant growth and straightness with a maximum gain in density gave a gain of 5.7% in density (75% of the maximum possible genetic gain).

4. DISCUSSION

4.1. Genetic determinism of wood quality traits and comparisons with other studies

For growth, straightness and wood heterogeneity, our estimated heritabilities correspond well with those found in previous studies of maritime pine and other coniferous species (growth and straightness: [12, 14, 31, 65, 67]; wood heterogeneity: [26])

Wood quality traits, including density and fibre properties, showed heritabilities that were generally lower than those reported in the literature. These results can hardly be attributed to the sample size (numbers of families and individuals within each family), which was consistent with samples used in these studies. The high sensitivity of maritime to deviation from verticality and its high within-ring variability in density compared to other conifers can probably explain these results. It is likely that the pronounced basal deviation induces additional environmental effects on maritime pine wood quality. Furthermore, the high within-ring variability in density, which probably reflects a higher sensitivity to climate, may also influence other wood characteristics, increasing environmental variances and consequently decreasing their heritabilities.

Although a significant heritability was found for mean density, no genetic effect was detected for indirect density estimation by pilodyn measurement. Similar results have been reported for Eucalyptus where heritabilities ranging from 0.16 to 0.23 were obtained for density measured indirectly by pilodyn, while heritabilities estimated for density measured on increment cores ranged from 0.67 to 1 [39]. Assessment of density by pilodyn does not seem relevant for maritime pine.

Table X. Index selection optimisation and consequences for "wood quality".

	Weights									Relative gain (% of maximum genetic gain) [a]								
Index	TH_adj	STR	d	het	lignin_adj	alfacel	coars	curl	zspan_adj	TH_adj	STR	d	het	lignin_adj	alfacel	coars [b,c]	curl [c]	zspan_adj [c]
A (17)	1	–17	0	0	0	0	0	0	0	65.27	50.91	–59.98	–54.69	–18.74	–15.57	63.98	–22.13	–5.37
B (20)	1	–17	5	0	0	0	0	0	0	1.49	43.77	52.73	–37.66	59.78	63.51	–20.72	64.38	–7.15
C (30)	1	0	7	0	0	0	0	0	0	1.15	–34.16	80.60	30.06	44.39	48.30	–58.03	70.00	–38.78
D (39)	1	–9	6	0	0	0	0	0	0	0.67	1.65	74.97	–0.89	56.78	60.94	–45.42	74.21	–26.36

[a] The sign of the relative gain correspond to the breeding success according to the tree breeders objectives. + means improvement, – means depreciation of the trait. In an ideal case all the relative gains would be positive.
[b] According to the genetic correlations observed in *table VII*, coarseness can be used here as a good predictor of fiber length and fibre width.
[c] Taking into account our poor knowledge of the consequences of modifying fibre properties for wood quality, increase of those traits were fixed arbitrarily as breeding objectives.

In agreement with other reports in the literature [10, 11, 15, 19, 60, 66], we observed moderate to high heritability for lignin and holocellulose content ($h^2_{ns\ (holocellulose)}$ = 0.359, data not shown). Furthermore, the decomposition of holocellulose into its components allowed us to detect a significant genetic effect for α-cellulose but not for hemicellulose. One possible explanation for those contrasting results is the lower level of phenotypic variation for hemicellulose content which did not allow us to detect significant variation among families. Thus, from a tree breeder's point of view, the easiest way to increase cellulose content would be the improvement of α-cellulose content. This is also of more industrial interest than an increase in hemicellulose content, since hemicellulose is often removed during the pulping process. Concerning extractives, for which no genetic effect was detected, opposite results were obtained in other species for which significant heritabilities were reported [13, 15, 60, 66].

The lack of genetic control observed for kraft pulping traits (residual alkali, kappa index and pulp yield) despite the agreement with previous results obtained in maritime pine [26, 42] is surprising. Indeed, it is inconsistent with the significant heritabilities obtained for lignin and α-cellulose contents. The results of this study may be explained by the pulping process itself (kappa number of 30) which could have resulted in a severe degradation of lignin and also of a part of the α-cellulose. Indeed, the phenomenon of degradation of the cellulose (peeling effect) can be observed below kappa 35 for maritime pine. This explanation is supported by (1) the lack of a genetic effect for kappa index, which is unexpected given the differences in lignin content between families and (2) the high heritabilities reported for pulp yield in other species. [15]. The values for kraft pulping parameters obtained in this study may be unrepresentative, and should be treated with caution.

4.2. Integration of wood quality in the maritime pine-breeding programme

4.2.1. Interesting single-trait genetic gains are expected

The main requirements of forest managers and pulp manufacturers can be roughly summarized as an increase in yield and an improvement in wood homogeneity. The heritabilities and phenotypic variation observed for height growth, straightness and density heterogeneity suggest that high genetic gains (reaching 11, 28 and 12% respectively) could be expected from independent selection for each of these traits.

However, final pulp and paper quality also depends on wood properties. And for traits such as density, wood chemical composition and fibre properties, expected genetic gains are lower (< 5%). However, given the volume of wood processed each year by the pulp industry and its predicted increase, even slight modifications of these traits could be of commercial value.

Several economic studies [5, 8, 37], have shown that density has a major impact on mill profits because it affects harvesting, transportation and milling costs. This conclusion is not really applicable to the French maritime pine pulp market where pulp companies buy wood by weight and not by volume. Still, breeding programmes integrating wood density would have great consequences for forest owners' profits, by increasing the mass of wood produced per hectare. Such breeding programmes are impeded by the lack of accurate, rapid and cheap tools for estimating density. In maritime pine, as in *Eucalyptus*, pilodyn measurements give poor estimates of density. Improvement of wood quality using density as the main target of selection is dependent on the development of new measurement tools.

The influence of density on pulp production and quality has been widely studied, but less is known about the links between fibre morphological properties and kraft pulp production. Horn et al. [24] stated that, for softwoods, there are no relationships between fibre length per se and any one sheet property. Others have shown that tracheid length and tracheid coarseness were the best predictors of costs for thermo-mechanical pulping and high brightness newsprint production [8]. Our results, suggest that improvement of morphological fibre properties is possible, but in order to justify large scale screening, studies will have to be done to define the effects of fibre morphology on kraft pulp production and quality in maritime pine.

Modifications of wood chemical composition and particularly a decrease in lignin content accompanied by an increase in cellulose content would be advantageous in (1) decreasing energy and chemical consumptions per unit of dry wood charged [46, 55] and (2) increasing pulp yield. Our results show that it is possible to obtain this type of result in maritime pine (e.g. –1 and +1 unit respectively for lignin and α-cellulose content). In this context the FTIR technique used in the present study may offer some advantages when compared with conventional wet chemistry methods. It is a rapid assessment technique, giving estimates, with reasonable precision, of the chemical composition of small wood samples, hence contributing to a reduction in measurement costs [11].

Although single-trait genetic gains are possible, improvement of the average of one trait will have consequences for other traits, which may in turn have significant impacts on pulp and timber production and quality.

4.2.2. Relationships between fibre properties and wood chemical composition

In the literature, fibre properties and the chemical composition of wood are acknowledged to be of great importance for the pulp and paper industries. Comprehension of the relationships between them is thus of primary interest in the development of a breeding programme aimed at improving pulp and paper quality.

The high positive genetic correlations observed between fibre morphology traits, including fibre length, fibre width and coarseness, suggest that the same set of genes is likely to be responsible for their control, allowing tree breeders to consider only one of the traits in order to improve all of them. The strong genetic correlation between fibre morphology and coarseness is in contrast to the non-significant to low correlation that is generally reported in the literature [30, 45]. But in one case [45], coarseness was measured in a different way, i.e. using wood density and cell wall dimensions. Therefore, the comparison should be considered with caution. Nevertheless, the positive genetic correlation that was obtained in the present study, is consistent with what is expected if increased fibre length results in fewer fibres per unit volume. The strong negative correlations between curl index and fibre dimensions are probably due to the lower flexibility of wider fibres.

Although Einspahr et al. [15] observed a positive correlation between fibre strength and fibre length in *Pinus elliottii*, no significant relationships were observed between zero span and the other fibre properties in our study. In maritime pine, genetic control of fibre strength seems to be independent of the genetic control of fibre morphology. Thus, if selection for fibre strength is important for paper properties, it will need to be considered independently of other fibre traits.

The only significant genetic correlations involving wood chemical characteristics and fibre properties were those between curl and α-cellulose, and between curl and lignin (0.567 and –0.54 respectively). These correlations could be explained by the rigidity conferred on the fibre by the deposition of lignin, though this hypothesis could be confirmed only if, after delignification, morphological characteristics of the fibre are conserved. A link between chemical content and microfibril angle (MFA) would explain the correlations between lignin, α-cellulose content and zero span in our study and be in agreement with the findings of Einspahr et al. [15]. Indeed, Chaffey [7] pointed out that the orientation of micro fibrils might well dictate the deposition patterns of lignin and it has been shown that MFA is an important factor in determining the strength properties of individual fibres [47].

In terms of breeding objectives, fibre morphology (length, width, coarseness), physical fibre properties (curl, zero span) and wood chemical composition have to be considered independently. But, as already discussed, the consequences of modifying fibre properties for final end products are not well understood, thus for the present, breeding programmes designed only to improve fibre properties are not appropriate. The main objective of tree breeders will almost certainly remain growth improvement, probably with the integration of wood density as a general selection criterion for wood quality. In the following sections we examine the consequences of selection for growth and density on other wood properties and the possibility of optimising wood quality within a breeding strategy.

4.2.3. Selection for growth and correlated responses on wood properties

Today, pulp and paper production account for one per cent of the world's total economic output. There is a rapid and steady increase in demand for pulp products and an increasing shortage of wood supplies. Hence short-rotation intensive culture plantations are now being actively researched as a source of mill furnish [58]. In this situation, one of the mains concerns of tree breeders is the relationship between growth traits and wood properties.

It is generally observed in maritime pine [4], that there is a negative genetic correlation (non significant in our case) between growth and straightness. As a result, selection for height only will result in an increase in basal sweep, which is associated in conifers with a higher frequency of compression wood, an undesirable characteristic in the timber and paper industries.

Unlike *Picea* (spruce) species, for which a negative genetic correlation is generally reported [52], the relationship between growth traits and wood density is variable in pines. Indeed for maritime pine, positive correlations were found by Polge and Illy [49] and Nepveu [40] while independence of these traits was reported by Keller [26] and Kremer and Nepveu (unpublished). In the present study, a negative correlation between height and density was observed. The differences between the studies can hardly be attributed to maturation effects, since trials giving conflicting results were of almost the same age. One explanation could be the existence of a considerable between and within–population variation for the relationship between growth and wood density in maritime pine. Such variation, partly of genetic origin, was found in Douglas-fir [53].

The absence of a correlation between growth and density heterogeneity has also been reported in other studies involving maritime pine [26, 41]. Selection of trees combining high growth potential with high wood homogeneity, two of the main requirements of pulp manufacturers and forest owners, is thus feasible.

As in *Picea sitchensis*, for which Costa E. Silva et al. [11] found a positive (unfavourable) correlation between growth and lignin content, unfavourable correlations between growth (height) and wood chemical composition were observed. Selection for increasing growth is expected to result in extra costs for pulping and lower pulp yields.

In agreement with what is generally reported in the literature, moderate positive genetic correlations between growth and fibre length [19–21, 30] and between growth and coarseness [30] were obtained.

It appears that breeding programmes, which aim to improve growth alone, will decrease both timber quality and the efficiency of pulp production. No definite conclusion can be drawn in respect to fibre morphology since objectives vary according to the final product.

Table XI. Hypothesis testing of the negative additive genetic correlations observed between fibre morphology traits (fibre length, fibre width and coarseness) and density.

Simulation number [a]	Ld/Cwt [b]	FL [c]	FW [d]	Coarseness [e]	Ld [f]	Cwt [g]	Lumen volume of one fibre [h]	NF [i]	Total lumen volume [j]	density [k]	r (d–fmorph) [l]	Consistency with our results [m]
1	**3**	20	2	5	1.50	0.50	70.65	**4**	282.60	=	0	no
	3	10	1	1	0.75	0.25	8.83125	**32**	282.60			
2	**2**	20	2	5	1.33	0.67	55.8222222	**4**	223.29	≠	–	yes
	1	10	1	1	0.50	0.50	3.925	**32**	125.60			

[a] (1) Identical lumen "diameter/cell wall thickness" ratio. (2) Different "lumen diameter/cell wall thickness" ratio .
[b] "Lumen diameter/cell wall thickness" ratio.
[c] Fibre length given in arbitrary unit.
[d] Fibre width given in arbitrary unit. The values were chosen according to the positive additive genetic correlation observed between fibre length and fibre width (*table VII*).
[e] Coarseness given in arbitrary unit. The values were chosen according to the positive additive genetic correlation observed between fibre dimensions and coarseness (*table VII*).
[f] Lumen diameter deduced from FW and Ld/Cwt.
[g] Cell wall thickness deduced from FW and Ld/Cwt.
[h] Lumen volume for one fibre calculated as: $2 \times p \times (Ld)^2 \times FL$.
[i] Number of fibres in a volume corresponding to 20 (length) $\times$ 4 (width) $\times$ 4 (depth) (in arbitrary unit).
[j] Lumen volume, corresponding to a total volume of 20 (length) $\times$ 4 (width) $\times$ 4 (depth), calculated as: (lumen volume for one fibre) $\times$ (NF). The bigger the lumen volume is, the lower the density is.
[k] Density, "=" means identical mean density for the two type of fibres, "≠"means different mean density for the two types of fibre.
[l] "Correlation" between density and fibre morphology traits (FL, FW, coarseness) obtained by simulation.
[m] Consistency between the correlations involving fibre morphology traits and density obtained by simulation, and the correlations obtained in our study .

4.2.4. Selection for density and its implications for other wood properties

The economic importance of density as a reliable, easy to measure trait that largely determines the suitability of wood for various end products is widely acknowledged [46]. Nevertheless, it is interesting to evaluate the extent to which selection for density affects other wood quality properties in maritime pine. For timber quality traits, no significant genetic correlations were observed between density, straightness and density heterogeneity. Similar results have been generally reported in various species [6, 11, 26, 34, 49], obliging tree breeders to consider these traits independently in the definition of the selection indices.

Strong genetic correlations of opposite sign were obtained between density and lignin (– 0.544) and density and α-cellulose (0.624). Similar results were obtained in *Picea sitchensis* where Costa E. Silva et al. [11] observed a negative relationship between density and lignin content. In spite of the composite nature of density which involved tracheid size, cell wall thickness..., it seems largely explained by the α-cellulose content of wood which is negatively correlated with lignin content. It has been often reported that lignin and cellulose content are respectively lower and higher in the latewood [32, 57, 61–64]. However our results did not allow us to conclude to a tight relationship between density and latewood percentage. Indeed, although fibres are longer in the latewood a negative genetic correlation was observed between density and fibre dimensions. In addition no genetic effect was detected for latewood percentage (data not shown). From a practical point of view, the correlations between density and wood chemical composition have interesting industrial implications: selection for increased density would at the same time increase pulp yield and decrease production costs.

Negative genetic correlations were obtained between density and fibre dimensions, consistent with observations reported by Nyakuengama et al. [44], King et al. [30] and Hannrup et al. [20]. A strong negative genetic correlation was also observed between density and coarseness, in contrast to results reported in previous studies [30, 44]. As mentioned previously, a comparative analysis should be considered carefully especially with the result obtained in [44]. Nevertheless, the negative genetic relationships found in this study could probably be explained, as shown in the *table XI*, on the one hand by the lower amount of fibre per unit volume in individuals producing long fibres, and on the other hand by their higher "lumen diameter/cell wall thickness" ratio.

A strong positive genetic correlation, which could be an indirect consequence of the higher flexibility of thin fibres, was reported between density and curl. In contrast, a correlation close to zero was obtained between density and fibre strength. This lack of genetic correlation will have to be considered if density is used as predictor for wood quality breeding.

Breeding programmes using density as the only selection criterion may lead to a severe reduction in height growth, an improvement of the lignin/α-cellulose ratio, a decrease in fibre dimensions and an increase of the curl index of fibres. For breeding purposes, density seems a useful indicator of wood chemical composition and fibre morphology, but a poor predictor of wood heterogeneity and fibre strength. Nevertheless, these results will need to be verified in other trials. Moreover, further studies will have to be performed in order to determine its relationship with commercially important paper properties.

4.2.5. Optimisation of breeding for wood quality

Simultaneous breeding for "wood quality", using density as the main selection criterion, while maintaining levels of gain in the traditional targeted traits is not realistic. An efficient way of integrating wood properties in the maritime pine breeding programme would be the creation of elite populations dedicated exclusively to improving wood quality for particular end uses. The current maritime pine-breeding programme is based on a breeding index including growth and straightness. In this study it is shown that its consequences for wood quality are significant and leads to a strong depreciation of many technological wood characteristics (density, chemical composition). Nevertheless these results can not lead to finite conclusions, further trials will be needed in order to estimate accurately and reliably the genetic control of wood quality and its relationships with other targeted traits. Furthermore, despite the reduction of density, the current selection allows important genetic gain for straightness and therefore in wood homogeneity, two important characteristics for timber and pulp industries.

A two-step procedure for wood quality improvement could be as follows: first selection for straightness and growth will ensure volume production and wood homogeneity; second, specific wood quality traits (e.g. density, lignin content) could be selected from the previous improved population. Genotypes would be selected, depending on the tree breeder's objectives, using index "B" or "D" (*table X*), which are both conservative with respect to growth. Index "B" is probably more suitable for timber production, allowing simultaneous improvement of straightness and density (+43 and 50% respectively of their maximum genetic gain). Index "D", which gives a greater increase in density and thus improves the lignin/α-cellulose ratio is better suited to pulp and paper production.

5. CONCLUSION

Our results suggest that breeding of maritime pine trees with outstanding wood quality is feasible. But several points need to be emphasised.

First, although this study allowed us to estimate heritability of several wood properties, these estimations were made for composite traits (total height, mean density, etc.), at a unique maturation stage. No information about maturation effects are available and time trend analysis of height, diameter growth and density components is a necessary future area of study.

Secondly, the correlations between basic wood properties and end product properties are often not well known. Genetic improvement of wood properties is possible, but before they are included as selection criteria in the maritime pine-breeding programme it is essential to determine their effects on the properties of different types of end product. Within the frame of a EU funded project (http: //www.pierroton.inra.fr/Gemini/), this work will be performed through measurements of pulp properties (tear index, burst index...), which have real meaning at the industrial level.

Thirdly, simultaneous breeding for traditional target and wood quality traits is compromised by adverse genetic correlations. As it was shown in this paper, the best way of integrating wood quality in the maritime pine breeding programme is probably the constitution of elite population dedicated exclusively to wood quality with trees selected in a growth-improved population.

Finally, despite the identification of possible target traits for breeding, the diallel analysis provided neither useful predictors for early selection, (it is not possible to evaluate these traits in very young trees), nor the exact genetic architecture of wood quality traits (number of genes, locations, effect of each gene). The latter point is being addressed through QTL (Quantitative Trait Locus) mapping, to identify the chromosomal regions involved in the genetic control of these traits. QTLs should provide not only fundamental information, but also potential early predictors of wood properties, thus avoiding the high costs of traditional measurements and reducing the age of assessment of the traits.

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